from a complete pre-nuptial moult. In a collection of skins it is possible to find a series which appears to show reduction of buff edges in a gradual succession from the eclipse to the full breeding plumage, and this has tended to conceal the existence of a complete moult between the eclipse and the breeding plumage.

The figures are diagrammatic sketches, not necessarily to scale, intended to show only the extent of the black and the buff (diagonally shaded)

colouring.

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Mottled plumage in the genus Corvus

by BRYAN L. SAGE

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C. J. O. Harrison (1963) has recently dealt with the subject of mottled plumage in various species of the genus Corvus, and concludes that this condition is not genetic in origin as originally suggested by Dr. James M. Harrison (1948) and the writer (Sage 1956), but is caused instead by periods of unbalanced diet affecting the rhythm of melanin deposition. Despite his lengthy treatment of the subject I am quite unable to see that he has produced any evidence definitely disproving the genetical theory. Whilst agreeing that the majority of discussion on the subject must perforce be largely theoretical, it may be said that the explanation of the condition as originally proposed is perfectly in accord with simple and orthodox genetics.

Since the publication of my last paper on this subject (Sage 1958) I have done further research on the matter with the result that some of my earlier views are somewhat modified. Furthermore, I feel that C.J.O.H. has included in his discussion several types of plumage variation (i.e. brown plumage, white wing-barring, and fault bars or "hunger traces") which I consider are not in fact analogous, thereby confusing rather than

clarifying the situation.

BROWN PLUMAGE TYPES

A mounted specimen of the Raven Corvus corax in the collection of the British Museum (Natural History) is described by C. J. O. Harrison (pp. 43-44) as being a dilute partial albino, having the feathers of the lower belly, forehead and throat loose and fluffy in texture, and the pigmented portions of the plumage grevish-brown. The fluffy texture of the plumage of this specimen, which I have myself seen, is presumably due to some defect in the interlocking mechanism of the barbules, the identical factor which gives rise to the "hairy" variety of the Moorhen Gallinula chloropus. It may be noted that in the Moorhen this condition is frequently, but by no means invariably associated with depigmentation of the plumage to a greater or lesser degree. I have in my possession a specimen of the Rook Corvus frugilegus given to me by the late Alfred Hazelwood of the

Bolton Museum. In this bird the entire plumage, with the exception of the wings and tail, is medium-brown in colour and fluffy in texture; the wings and tail are almost normal but the feathers are whitish terminally to a varying degree. I consider the fluffy or "hairy" plumage condition to be genetically determined. As a further example of the former condition I would include the Carrion Crow Corvus corone that I originally described (Sage 1956a) as an example of the mottled type of plumage; the wing of this bird was uniformly brownish.

It is a well known fact, as I stressed in 1956, that a defective diet can produce in captive corvids (and probably other species as well) a uniformly brown or partially depigmented plumage. The condition occurs in young birds and also in adults, in the latter case most usually at the period of moult. At a later date the plumage reverts to the normal colour. During the process of moulting a bird is under considerable physiological strain and it may need only a very slight deficiency in diet at this time to upset the process of pigmentation of the growing feathers. An adult Rook that I shot in October 1961 near Hertford had the plumage entirely normal with the exception of the head and neck, the feathers of which were two differing shades of brown resulting in a mottled appearance. The head plumage is the last to be moulted in the change from summer to winter plumage in this species, and I infer that in this instance the moult had progressed normally until the final stage, at which point some physiological factor caused the abnormally pigmented feathering. Other records of adult corvids in this type of plumage exist. It may also be noted that in some years, e.g. 1951 and 1954, both brown and mottled examples have been found together in the Ashwell rookeries, and the former have also occurred in years (e.g. 1952) when no mottled mutants were present. I shall return to the significance of this point later on.

It remains only to say that I do not consider either the "hairy" type of plumage or the partially or completely depigmented brown type to have any connection whatsoever with the mottled plumage sens. strict of the Rook. The fact that a combination of these conditions may sometimes

occur in one individual does not affect this point at all.

WHITE WING-BARRING

The second type of plumage variation included by C.J.O.H. in his overall discussion is that of white wing-barring in the Carrion Crow and Jackdaw Corvus monedula, as recorded by Dr. James M. Harrison (1957a & b) and the writer (Sage 1956c). I agree with J.M.H. that this is probably a condition of comparatively recent origin compared with the mottled plumage of the Rook which has been known for a great many years, and also that it is remarkably stable in pattern. The white wing-barring in the Carrion Crow is now certainly widespread as I have received a good many reports from quite different localities. Furthermore, my own studies have produced pretty clear evidence that this condition can persist unchanged through the various moults into adult plumage. At the time of writing there are at least nine adult Carrion Crows in my own district that exhibit this type of plumage pattern.

It seems fairly evident that this condition is genetically determined: if it were due to a period of unbalanced diet it would be extremely unlikely to persist into adult plumage. Additionally, I find it hard to imagine that

Carrion Crows in a number of widely scattered localities not only suffer from a defective diet, but as a result also exhibit an exactly similar pattern of plumage variation. There appears to be an almost complete lack of any record of white wing-barring being produced in conditions of captivity as a result of faulty diet. The only exception, as mentioned by Dr. James M. Harrison (1962) is that Fritz, Hooper, Halpin and Moore (1946) have shown that a deficiency of lysine can produce symmetrical white wing banding in bronze-wing turkey poults. It does not follow, however, that this is the explanation of the variant plumage in the Carrion Crow and Jackdaw. In the broods of young Carrion Crows where white wing-barring has been noticed, there have been some normal birds present also. Presumably all have been similarly fed, so that if the wing-barring is caused by a defective diet it would be necessary to postulate a selective suscepti-

bility to this factor; this is surely highly improbable.

C. J. O. Harrison when discussing this particular aspect says "The former species (i.e. Carrion Crow) seems particularly prone to such defects, especially in urban or suburban areas where the principle feeding places are often rubbish tips, and the diet is likely to be abnormal or deficient." The known facts, however, do not support this contention. In the first place in those areas where corvids habitually feed on rubbish tips, the habit can hardly be described as abnormal. Secondly, it so happens that all the records in my own area of white wing-barring refer to birds that are entirely rural in their habitat, and the same is true of quite a large proportion of records that I have received from other areas. Dr. J. M. Harrison (1957b) suggested that this plumage aberration may be due to inbreeding in a population that has increased due to a lack of predation or other control. This may well be the case, as there are numbers of aberrant Carrion Crows in the vicinity of Hilfield Park Reservoir, Hertfordshire, which have almost certainly originated in this manner. In 1960 and 1961 a pair of this species reared three and two young respectively, all with white wing-barring. In 1962 two pairs bred at the reservoir; one pair in the same tree as in the two previous years produced two young with white wing bars; the second pair (one of which was barred and was probably one of the birds reared in 1961) nested some 300 yards distant, and two of their three young were barred on the wings. All these birds are still about. There is no question of the population density in this area being so great as to make it difficult for the birds to obtain normal food. C.J.O.H. places what I consider to be too much faith in the evidence provided by nutritional disorders in captive birds. The white banded wing type reported in the turkey by Fritz et al is probably morphologically similar to the white wing-barring in the Carrion Crow and Jackdaw, but the evidence I have given above shows, in my opinion, that the factors responsible cannot be the same.

FAULT BARS AND DIET

The next point requiring discussion is that concerning fault bars or "hunger traces". So far as they are concerned there appears to be no evidence of consistent correlation with mottling or barring of the feathers. In the past five years or so I have examined several hundred young Rooks and somewhat lesser numbers of young Crows. In the great majority of cases at least a few fault bars were found, sometimes on one or two

feathers only. In other cases virtually all of the wing and/or tail feathers exhibited them. Out of a total of 430 young Rooks examined, 32 had a narrow pale band(s) associated with the fault bar(s), in some instances this bar was no more than fractionally paler than the rest of the feather. On the other hand there were some 57 individuals which had narrow bands of less heavily pigmented areas on the feathers of the wings and/or tail which were totally unrelated to the presence of fault bars. Practically every one of the remaining 341 birds had narrow transverse bars on some feathers of the wings and/or tail, occasionally also on the body plumage. In the majority of cases the inhibition of pigmentation was so slight that the bars could only be detected with great difficulty. There is nothing new in this. Glegg (1944) called them latent or subordinate markings and found them on every one of 935 specimens that he examined. It seems quite unnecessary to invoke any explanation for this phenomenon other than that the bars are caused by the lower metabolic rate or decreased blood pressure during the hours of darkness, as suggested by Riddle (1908).

The above evidence, based on a large random sample, of the lack of correlation in the siting of fault bars or "hunger traces" and the pale bars caused by reduced pigmentation clearly negatives the comment made by C. J. O. Harrison on page 45 of his paper, where he comments on "... the apparent relationship between such bars and hunger traces." This relationship is not apparent to me. It hardly seems necessary to add that I do not consider the often strikingly pale and broad transverse barring or tips to the feathers found in the mottled variety of the Rook (in extreme cases on the entire body plumage) to be analogous with the type of pale bars discussed above. It may also be added that the latter may often be found, along with fault bars or "hunger traces", on individuals of the

mottled type.

Further evidence quoted by C.J.O.H. as analogous to the Rook problem are the experiments of Rollin (1959) who reared Blackbirds Turdus merula in captivity on a thoroughly abnormal diet, the basic component of which was dog biscuits, and found that new feather growth was greyish or whitish. I regard this comparison as ludicrous in the extreme as a diet so markedly abnormal could hardly fail to have some effect, but I have yet to see or hear of any evidence proving that wild birds have to subsist for long periods on an extremely abnormal diet. Furthermore, the markings on Rollin's birds had little resemblance to those found on the variant Rooks discussed here. Although these dietetic experiments under avicultural conditions are interesting, I feel that their relation to natural populations is somewhat doubtful and interpretations of this nature should be subject to caution. As mentioned earlier, aviculturists have often found that various species of Corvidae will assume a brown type of plumage if their diet is deficient. It is probably reasonably safe to assume that this factor is also responsible for the brown-plumaged Rooks, Crows, and Jackdaws sometimes seen in the wild, but this has never been definitely proved.

At one time I gave serious consideration to the theory that abnormal feeding conditions were the cause of mottled plumage in the Rook. It has been suggested that very dry springs, as in 1959 when young Rooks of this type were present in the Ashwell rookery on the Herts/Cambs border, may make it difficult for the adults to obtain proper food for the young. I

therefore listed all the years when mottled Rooks had been found anywhere in the British Isles and checked them with the meteorological reports; I was unable to find any consistent correlation. I see no reason to suppose that where an important item in the diet of Rooks, e.g. Lumbricidae, are hard to obtain, that a satisfactory alternative cannot be found. Indeed, a specific instance of this is mentioned by Owen (1959). On page 48 of his paper C.J.O.H. refers to 'The individual bird which consistently fails to rear or feed its young properly, year after year, is known to aviculturists.' Do such cases always have an effect on the pigmentation of the plumage, and has anyone definitely proved that this occurs in wild corvids? I think not. The young of the Rook hatch asynchronously, with the result that when food is scarce the smallest young die of starvation.

Let us accept for the moment that the mottled type of plumage in the Rook is in fact due to a diet deficiency. At the Ashwell rookery careful records have been kept over a long period, and the incidence of such birds has rarely been higher than 1%. As this is based on the number of mottled birds found amongst the birds that are shot, the actual incidence is probably even lower. In view of the strong tribal feeding habits of this species it seems illogical to suggest that a food deficiency would affect only an extremely small proportion of the population. Why, also, should this supposed shortage of food occur with such frequency at the Ashwell rookery, which is situated in a highly fertile area, and not at other rookeries? To take the matter further, let us also accept that the brown plumage type found in wild corvids is, as mentioned earlier, analogous with that found in captive birds. In some years both this and the mottled type are found simultaneously at the Ashwell rookery. Are we therefore to believe that a food shortage results in the occurrence of two entirely different types of plumage variation? This, to my mind, is completely unacceptable. It might also be mentioned that although corvids are fairly often kept under avicultural conditions, there appears to be no case on record of a mottled type being bred in captivity.

Finally, if the factors responsible for the mottled plumage condition are in fact those stated by C.J.O.H., then surely the condition would be much more frequent and widely distributed than is the case. On the other hand if the causative factor is a rare recessive gene(s), then its persistence in one relatively isolated group of rookeries, with occasional outbreaks at other localities is quite logical. It is probable that gene flow between widely separated rookeries is rather restricted. As far back as Millet (1828) it was suggested that this condition was an inherited character.

SUMMARY

The subject of mottled plumage in the Rook is discussed, and it is suggested that this condition is not analogous with other types of variation such as abnormal brown pigmentation, white wing-barring as found in the Carrion Crow and Jackdaw, and fault bars or "hunger traces". It is considered that mottled plumage is not caused by an unbalanced diet as suggested by C. J. O. Harrison (1963), and that no evidence disproving the original theory of a genetical basis for this condition has been produced.

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Further comments on hybridisation between the European Wigeon and Northern Shoveler

by James M. Harrison

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In 1959 the writer was able, through the generosity of Captain C. R. Peacock, to comment upon the characters presented by crossing a male European Wigeon (Anas penelope Linnaeus) and a female Northern Shoveler (Anas clypeata Linnaeus), an instance of a cross in which the exact parentage and age of the individual was known (Harrison, 1959). 1 Again thanks to Captain Peacock I have been able to investigate the sibling of the above mentioned specimen, which presents a marked variation in facial pattern, though in other respects very similar, while additionally I have been favoured with a third specimen presenting characteristics so closely approximating to those of the instance reported in 1959 (loc. cit.) and its sibling as to suggest that the same parent species were involved. The resemblances in fact between the first example and the last one mentioned, for which I am indebted to The Wildfowl Trust, are such that there would appear to be no reasonable doubt that the individual is also a European Wigeon x Northern Shoveler hybrid.

Dealing with the sibling individual first; this bird was hatched in the spring of 1957 and was presented to me in October 1962. It was kept alive